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ORIGINAL RESEARCH

Pictures or pellets? Comparing camera trapping and dung counts as methods for estimating population densities of ungulates

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Abstract

Across the northern hemisphere, land use changes and, possibly, warmer winters are leading to more abundant and diverse ungulate communities causing increased socioeconomic and ecological consequences. Reliable population estimates are crucial for sustainable management, but it is currently unclear which monitoring method is most suitable to track changes in multi-species assemblages. We compared dung counts and camera trapping as two non-invasive census methods to estimate population densities of moose *Alces alces* and roe deer *Capreolus capreolus* in Northern Sweden. For camera trapping, we tested the random encounter model (REM) which can estimate densities without the need to recognize individual animals. We evaluated different simplification options of the REM in terms of estimates of detection distance and angle (raw data vs. modelled) and of daily movement rate (camera trap based vs. telemetry based). In comparison to density estimates from camera traps, we found that, dung counts appeared to underestimate population density for roe deer, but not for moose. Estimates of detection distance and angle from modelled versus raw camera data resulted in nearly identical outcomes. The telemetry-derived daily movement rate for moose and roe deer resulted in much higher density estimates than the camera trap-derived estimates. We suggest that camera trapping may be a robust complement to dung counts when monitoring ungulate communities, particularly when similarities between dung pellets from sympatric deer species make unambiguous assignment difficult. Moreover, we show that a simplified use of the REM method holds great potential for large-scale citizen science-based programmes (e.g. involving hunters) that can track the rapidly changing European wildlife landscape. We suggest to include camera trapping in management programmes, where the analysis can be verified via web-based applications.

Introduction

Species-level estimates of population density are fundamental, both for the management and conservation of wildlife populations and for the understanding of ecosystem dynamics (Noon et al. 2012; Caravaggi et al. 2016). Across the northern hemisphere, ungulates have been rapidly increasing in numbers (Apollonio et al. 2010) and exert a profound sociocultural, ecological and economic impact (Sandström 2012). Many regions, particularly in Europe, now host diverse communities of up to four or five ungulate species, where only one or two species

occurred a few decades ago (Apollonio et al. 2010). Management goals are thus increasingly focused towards multi-species or ecosystem-based approaches (Latham 1999; Weisberg et al. 2002). This creates a challenge for monitoring as many census methods are species or habitat specific (Singh and Milner-Gulland 2011). For example, aerial surveys have often been described as the most accurate method for moose *Alces alces* (Boyce et al. 2012; Rönnegård et al. 2008), but the method is unsuitable for smaller species like roe deer *Capreolus capreolus*. Although numerous methods have been developed for monitoring ungulates, most studies have sought to identify the optimal method for one species (Mysterud et al. 2007; Rönnegård et al. 2008; Månsson et al. 2011), rather than a multi-species approach.

The most commonly used monitoring method for a wide range of ungulate species is counting of dung pellet groups (hereafter referred to as dung counts). The inference of population density from the correlation between dung counts and the number of individuals is well established (Eggert et al. 2003) and has been described as one of the most accurate methods for determining abundance (Plhal et al. 2014). However, dung counts can be problematic in multi-species ungulate communities due to seasonal variation of dung morphology (Alvarez 1994), varying encounter rates for pellets from differently sized ungulates (Lioy et al. 2015) and incorrect species assignation (Yamashiro et al. 2010).

In recent years, the use of camera traps has become increasingly popular for monitoring wildlife abundance and community structure (Burton et al. 2015). An advantage of camera trapping compared to dung counts, particularly for multi-species systems, is that it produces clear evidence of species identity. However, until recently the use of camera traps to produce reliable population estimates was limited to mark–recapture techniques, which rely on the recognition of individuals (Karanth 1995). This limitation has restricted the use of camera trapping for population estimates of most ungulate species (Rowcliffe et al. 2008). Although camera traps may provide indices of relative abundance, such as detection rates, these have been criticized for their implicit assumption of constant detectability across habitats, time and species (Harmsen et al. 2010; Sollmann et al. 2013). However, ongoing improvements in this field may improve abundance estimates from occupancy-based methods (Ahumada et al. 2013). Rowcliffe et al. (2008) suggested a random encounter model (REM) for estimating densities from camera trap data which does not require the recognition of individuals. Instead, the method is based on estimates of contact rates between animals and camera traps (Cusack et al. 2015). Since the first publication in 2008, the REM has undergone continuous development (Rowcliffe et al. 2014, 2016) and has been applied to a range of species (Rovero and Marshall 2009; Manzo et al. 2011; Zero et al. 2013; Carbajal-Borges et al. 2014; Cusack et al. 2015; Caravaggi et al. 2016). These studies have also investigated various challenges in parameterizing the REM with a number of solutions emerging. The most sensitive model parameter is the average speed of animal movement which can be estimated directly from camera images or from external data sources like telemetry (Caravaggi et al. 2016).

Our study compares population density estimates from camera trapping versus dung counts of four coexisting ungulate species – moose, roe deer, red deer *Cervus elaphus* and fallow deer *Dama dama* – in an area of Northern Sweden. All four species are difficult, if not impossible to individually recognize from camera images providing the opportunity to implement and evaluate the REM model. Our objectives were (1) to test which method would be most suitable for monitoring multi-species ungulate communities, (2) to test how density estimates derived with the REM compare with widely applied dung counts and (3) to develop a method that assures realistic estimates of density but that can still be easily performed by a range of people from volunteers to wildlife managers. This last objective is particularly important as citizen science programmes are becoming increasingly incorporated into monitoring programmes (Silvertown 2009). Given the ongoing developments of the REM, we evaluated how density estimates are affected by the method of determining the average speed of animal movement, that is, directly from camera images versus from telemetry data. We also used the camera's angle and the position of the animal to estimate average detection angle (ADA) and average detection distance (ADD), in comparison to the effective detection angle (EDA) and effective detection distance (EDD) using a distance sampling approach (Rowcliffe et al. 2011). We discuss sources of bias for both the REM and dung counts, and make recommendations for methodological improvements that would benefit the conservation and adaptive co-management of multi-species ungulate communities.

Materials and Methods

Study area and overall design

We estimated ungulate densities on Järnäshalvön, a peninsula that encompasses *c.* 200 km^2 in the northern Swedish province of Västerbotten. The area is characterized by a mixture of boreal forest, mires and agricultural land and constitutes one of the rare examples in northern Europe where the four deer species moose, roe deer, red

deer and fallow deer coexist. The study area is surrounded by the Bothnian Bay on three sides, except to the north where it is delimited by a fenced highway and railroad, as well as the towns of Nordmaling and Hörnefors (Fig. 1). Due to these major dispersal barriers, we assumed that there was limited movement of individuals of all species between the study area and the mainland. To confirm this assumption, we placed a camera on both banks of the Öreälven river which is the least disturbed potential corridor for animals moving in and out of the study area. For both census methods, we randomly placed 11 hollow grids (1 × 1 km) consisting of 16 evenly spaced sampling plots across the study area (Fig. 1). Sampling at fixed coordinate locations within a random grid ensured the comparison of the two methods with each other. The sampling plots included all types of non-urbanized habitats in the study area in an unbiased manner due to the random placement of the hollow grids.

Dung counts

Between 2 and 22 May 2016, directly after the snowmelt, we counted the number of dung pellet groups of moose, red deer, roe deer, and fallow deer in all sampling plots within a 5.64-m radius from the plot centre (plot size = 100 m^2). We excluded seven plots as they were positioned in lakes, flooded areas or private gardens. Pellet groups were assigned to species according to their morphological characteristics. However, due to difficulties in distinguishing between roe deer and fallow deer pellets, we used the number of pellets per dung group as a decision criterion. Pellet groups with ≤45 pellets were considered as roe deer and groups containing >45 pellets as fallow deer (Edenius 2012). Because the plots had not been cleaned of old pellets prior to the beginning of the study, we only counted dung that was deposited no earlier than the previous autumn by excluding highly decomposed pellet groups or those that were hidden

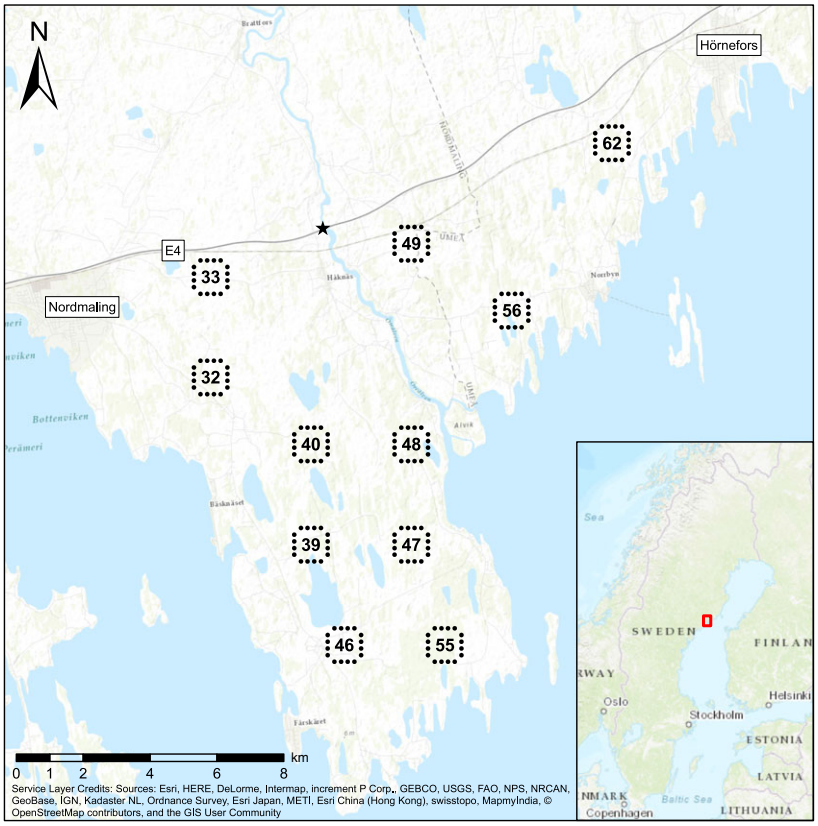

Figure 1. Study area on the Järnäshalvön peninsula. Eleven randomly placed hollow grids (classified as no. 32, 33, 39, 40, 46, 47, 48, 49, 55, 56 and 62) with 16 sampling plots (black points) along the grid boundary. Grids were on average 1.8 km apart from each other, with the exception of the central part of the peninsula where several lakes and rivers prevented this equal spacing. Sampling plots along the grid boundary were 200 m apart from each other. The black star represents cameras at the Öreälven river. The grey line in the north denotes the fenced highway E4 with the adjacent railroad track.

underneath a layer of leaves. We estimated species densities D (km^{-2}) (Cederlund and Liberg 1995) as,

$$D = \frac{n}{a * t * d}$$

where n denotes the number of pellet groups counted, a the total sampled area (km^2), t the accumulation period of dung (days) and d the daily defecation rate of each species (day^{-1}). We estimated the accumulation period t to be 215 days–from first leaf fall in autumn 2015 (Bergström et al. 2011) to mean date when dung was counted. Defecation rates may vary temporally and spatially for a given species. Therefore, we based our density estimates on rates taken from the literature, that is, 14 pellet groups per day for moose (Persson et al. 2000; Rönnegård et al. 2008) and 20 for roe deer (Mitchell et al. 1985), but we also provide density estimates using a range of defecation rates that have been recorded, with 13–23 for moose (Andersen et al. 1992; Persson et al. 2000; Matala and Uotila 2013) and 17–23 for roe deer (Mitchell et al. 1985).

Camera trapping

We randomly selected 12 of the 16 sampling plots in each of the 11 grids to monitor with camera traps. We excluded plots where cameras could not be adequately mounted on existing trees, that is, lakes and fields. Due to restrictions in our camera trap permit, we also could not place cameras in plots that were <100 m from human habitations or public roads. At each predefined sampling plot, a location was chosen with at least 10 m of open view in front of the camera to prevent natural features (e.g. large boulders, fallen trees) from obstructing detection. In doing so, we tried to stay as close as possible to the predefined location. Following these criteria, only 6 out of the resulting 132 camera locations had to be offset by more than 100 m from their intended coordinates. Two infra-red-triggered camera models were available, Reconyx Hyperfire HC 500 (n = 20) and HCO ScoutGuard SG 560C (n=15) (see Table S1 for detailed differences between the camera models). To monitor all 132 sampling plots, we used a rotation scheme of 12 days beginning on 7 March and ending 20 May 2016. Cameras were placed simultaneously in two sampling plots per grid (i.e. 22 sampling plots were monitored per rotation) and required six rotations to monitor all 132 sampling plots. To prevent any biases due to camera performance, the camera models were evenly distributed among sampling plots so that no grid was being monitored by only one camera model. To account for possible bias resulting from individual cameras, we randomly introduced four new cameras of each model into the pool of camera traps during each rotation event. However, two ScoutGuard cameras had to be replaced with Reconyx cameras during the study due to problems with camera functioning in direct sunlight. Cameras were mounted on a tree at a height of 1 m pointing towards a spot with at least 10 m of open view, where signs indicated that ungulate detection might be possible (e.g. game trails, tracks in the snow, forest gaps). We chose a height of 1 m to prevent cameras being covered by fresh snowfall and measured snow depth within the cameras' field of view when mounting the camera. Finally, we marked distances of 5 m, 10 m and 15 m in front of the camera's central field of view with small red ribbons in trees (Fig. 2). When triggered, both camera models took three photos in rapid-fire mode. Since there was no delay between the trigger sessions, the full passage of an animal through the cameras' detection zone was recorded. Additionally, we set the cameras to take daily control photos to confirm that all cameras remained operational throughout the 12 days.

Random encounter model

To estimate population density D (km^{-2}) from the camera trapping data, we used the REM proposed by Rowcliffe et al. (2008),

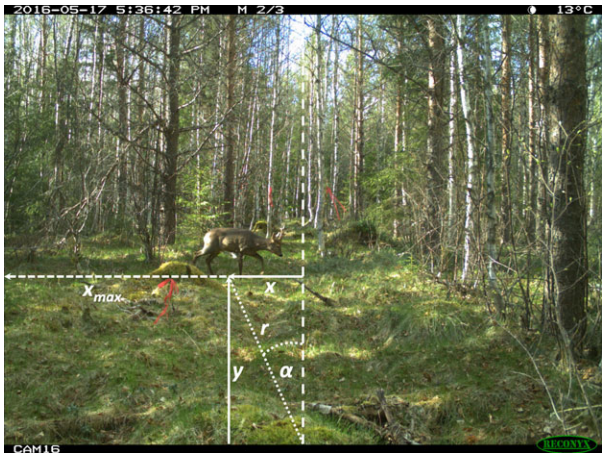

Figure 2. Example picture (Reconyx HC 500) of a male roe deer taken with red distance markers at 5, 10, and 15 m. The white dashed line in the centre field of view was used as reference point for distance calculations. r represents distance between the camera and animal (white dotted line) and α the angle of first detection (white dotted angle). Both were calculated trigonomically via the vertical and horizontal distances y and x (white arrows), where $r^2 = x^2 + y^2$ and $arctan(\alpha) = y/x$. For each vertical distance y, the maximum horizontal distance x_{max} (white dashed arrow) could be estimated based on the maximum angle of the cameras lens (extracted from camera manual). Via the centimetre ratio between x_{max} and x on the photo, x could be calculated.

$$D = \frac{y}{t} * \frac{\pi}{v * r * (2 + \theta)}$$

where y denotes the number of capture events, t the survey effort (camera trapping days), v the average daily distance travelled (km/day), r the ADD (km) and θ the ADA (radians). Approximately 50 captures per species are recommended as a minimum for reasonable REM density estimates (Rovero et al. 2013). Since we were interested in an overall population density across the study area, we pooled the camera trapping data across all grids to achieve this sample size. We defined a capture event as the first photo of an individual entering the camera's field of view (Rowcliffe et al. 2011) and determined detection distance and detection angle trigonomically using an adaptation of Caravaggi et al. (2016). The squared detection distance r^2 is the sum of the squared vertical distance y^2 and the squared horizontal distance x^2 to the animal based on the centre line of the cameras view (see Fig. 2). The angle of first detection θ was calculated as two times the arctan (α) ratio of the vertical and horizontal distance y and x respectively. For each vertical distance, we used the maximum angle of the camera lens (Table S1) and the centimetre ratio on the photo to estimate the horizontal distance. We estimated the distance and angle at which animals were detected using two different parameters to be able to compare the effect of the estimation method on density estimates. We calculated ADD and ADA by averaging detection distances and detection angles, respectively, across all capture events per species. In addition, we modelled EDD and EDA using a distance sampling approach (Rowcliffe et al. 2011). For each species, we fitted detection probability functions (half-normal models with and without a cosine expansion term) to our measured distance and angle data using the R package *mrds* (Laake et al. 2014). We used a point detection model to estimate EDD and a line detection model to estimate EDA (Rowcliffe et al. 2011). We tested for the effect of camera type by including it as a covariate in the species-specific model. Finally, we estimated densities for each species based on EDD and EDA as well as ADD and ADA and compared both approaches.

For estimating the mean distance travelled per day, v, we used both telemetry data (see next section) and inference from the camera trapping photos. For the latter, v can be interpreted as

$$v = s * a$$

where s is the daily distance travelled (km/day) if the species would be active the whole day [derived from the average speed (m/sec) at which animals moved in front of the cameras] and a the proportion of the day when a species is active (activity level as defined by Rowcliffe et al. 2016). Speed s_i is defined as,

$$s_i = \frac{d_i}{t_i}$$

where d_i is the distance (m) walked over a certain period of time t_i (sec) in front of the camera. The walked distance d_i per capture event was visually estimated from the photos as the distance between the animal's positions in all photos of a capture event. Time t_i was calculated as time between the first and last photo in a capture event accounting for animal movement (see Rowcliffe et al. 2016 for detailed description). The daily proportion of time spent active, a, was estimated per species as shown in Rowcliffe et al. (2014) using the R package *activity* (Rowcliffe 2016) which fits probability density functions to frequency data from the capture events. We used the bootstrapping option available in the *activity* package with 10,000 iterations to obtain 95% confidence limits and Wald tests to check for differences in activity patterns among the species. In northern latitudes, the progression of sunrise and sunset flattens activity peaks when using clock time (since ungulates are most active around dawn and dusk), which leads to an overestimation of activity levels (Rowcliffe et al. 2014) and thus an underestimation of density. We therefore transformed clock time to sun time using the code provided by Nouvellet et al. (2012) with the mean sunrise and sunset times of the study period serving as reference points. To determine the 95% confidence limits for the REM density estimates we bootstrapped with 10,000 iterations from the original data.

Using telemetry data to estimate average distance travelled

Following previous authors (e.g. Caravaggi et al. 2016), we also estimated the mean distance travelled per day, v, from GPS telemetry data. We used data from seven moose and four roe deer that had been tracked in our study area from early 2017. For the analysis, we extracted GPS data from March 2017 to May 2017, the same months as our camera trapping period. Unfortunately, no GPS data were available for red deer and fallow deer. The frequency of GPS locations may influence estimates of distance travelled per day due to the way that straight lines are drawn between recorded GPS locations. To determine how GPS position recording intervals influence the estimate of total daily movement rate, we split the data into time intervals that ranged from the highest available resolution (30 min for moose, 1 h for roe deer) to a low of 6 h intervals. Based on the R^2

value, we fitted a third-order polynomial regression model to the data in which the intercept indicated the presumed full day range, that is, if the tracking had been continuous. These values were then used in the REM for moose and roe deer respectively. All analyses were carried out using the program R (R Core Team 2016) with a significance level of $\alpha = 0.05$ for statistical tests.

Results

Dung counts

In total, we counted 88 dung pellet groups of ungulates (moose: $n = 45$, roe deer: $n = 25$, red deer: $n = 4$, fallow deer: $n = 14$). Due to the low sample size, red deer and fallow deer were excluded from further analysis. Density estimates derived from dung counts were 0.88/km^2 for moose and 0.34/km^2 for roe deer. When applying a range of defecation rates for both species, density estimates were 0.54-0.95/km^2 for moose and 0.30-0.40/km^2 for roe deer (Table 1).

Camera trapping

Over a period of 1584 camera trapping days, we recorded 174 capture events of the four ungulate species (moose: $n = 54$, roe deer: $n = 69$, red deer: $n = 45$, fallow deer: $n = 6$). We only detected four roe deer and one fallow deer leaving or entering the study area via the Öreälven river valley. Mean snow depth was 6.96 cm (min = 0 cm, max = 30 cm) during the study period. In 15 capture events, the species could not be identified on the photographs. Since the number of capture events for fallow deer and red deer did not meet the threshold of 50 capture events recommended for the REM by Rovero et al. (2013), we again excluded both species from the analyses.

Ungulate activity patterns generally showed a bimodal distribution which was especially pronounced for roe deer (see Fig. S1). Activity peaked around mean sunrise (05:01:17) and mean sunset (19:53:40). Daily activity levels varied slightly between moose (0.38) and roe deer (0.41; see Table S2), but differences were not significant (Wald tests, $P > 0.05$).

The daily distance travelled by moose estimated via GPS telemetry data (Fig. 3) was 2.08 km which yielded an REM density estimate of 2.50 moose/km^2. For roe deer the daily distance travelled was estimated as 4.22 km which converts to a density estimate of 2.36 roe deer/km^2. The estimated daily distance travelled for moose from the camera trap footage was 8.59 km, while it was 11.90 km for roe deer (Table 1). The basic REM density estimates based solely on data from the camera trapping photos (ADD and ADA values) resulted in 0.61 moose/km^2 and 0.84 roe deer/km^2. Similar density estimates were obtained when using the EDD and EDA with 0.60 moose/km^2 and 0.73 roe deer/km^2. Model comparisons showed that models including camera type as a covariate did not perform better than models that did not include camera type, except for the species-specific estimate of EDD for moose (ΔAIC = 3.91). For consistency, we thus decided to exclude the camera type as covariate. Model parameters and density estimates are summarized in Table 1.

Discussion

Monitoring animal populations and thus estimating population densities are essential for managing wildlife, and dung counts may be a useful, simple method for a wide range of ungulate species (Cromsigt et al. 2008).

Table 1. Sample size *n*, distance, angle, day range and density estimates for moose and roe deer in Northern Sweden based on four different approaches: dung counts, REM when estimating the average detection distance (ADD) and angle (ADA) from camera trapping images, REM when estimating effective detection distance (EDD) and angle (EDA) via a modelling approach and REM when estimating day range based on telemetry data.

						Density (per km^2)			
Approach	Species	*n*	Distance (m)	Angle (radians)	Day range (km/d)	Estimate	SD	95% CI	PRP
Dung counts	Moose *Alces alces*	45	–	–	–	0.54–0.95	–	–	–
	Roe deer *Capreolus capreolus*	25	–	–	–	0.30–0.40	–	–	–
ADD and ADA	Moose *A. alces*	54	8.24	0.50	8.59	0.61	0.06	0.44–0.66	18.10
	Roe deer *C. capreolus*	69	5.59	0.45	11.90	0.84	0.08	0.70–1.01	18.57
EDD and EDA	Moose *A. alces*	54	8.16	0.58	8.59	0.60	0.05	0.49–0.70	16.95
	Roe deer *C. capreolus*	69	5.51	0.86	11.90	0.73	0.06	0.66–0.89	16.28
Telemetry	Moose *A. alces*	7	8.24	0.50	2.08	2.50	0.23	1.82–2.72	18.00
	Roe deer *C. capreolus*	4	5.59	0.45	4.22	2.36	0.23	1.98–2.87	18.86

PRP represents the percentage relative precision according to Sutherland (2006).

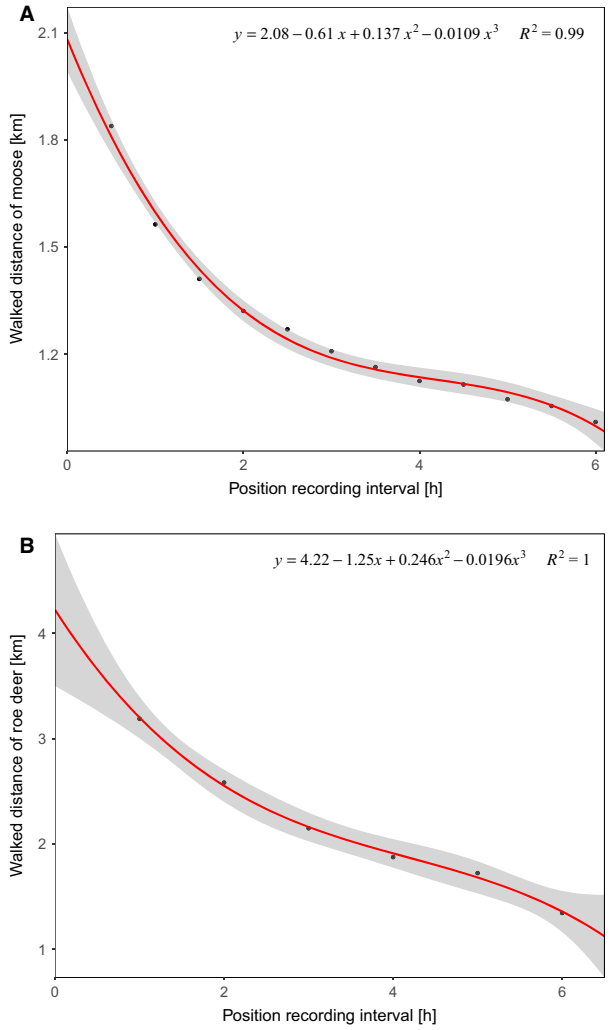

Figure 3. Estimation of daily distance travelled for (A) moose and (B) roe deer in Northern Sweden based on a third-order polynomial regression model fitted to 30 min and 1 h GPS collar positioning intervals, respectively. The intercept with the *y*-axis indicates the day range of the species. The slope most notably declines within the first 120 min suggesting that the time intervals between recorded positions strongly influence day range estimates.

However, there are valid concerns that species may be incorrectly identified based on dung morphology (Yamashiro et al. 2010), especially where several similarly sized ungulates coexist. There are also biases towards detecting species with larger pellets and intra-specific variation in dung morphology among seasons or landscapes puts further limits on the method (Alvarez 1994). Several studies have demonstrated that density estimates from dung counts correlated well with direct counts (red deer: Batcheler 1975; fallow deer: Bailey and Putman 1981). In our study, density estimates of moose were similar between the REM and dung counts, and these slightly over- or under-estimated the current official estimate of 0.78 moose/km^2. This estimate was calculated by Svensk Naturförvaltning AB (2016) based on bag statistics and moose observation data. When considering how defecation rates might vary by habitat or season, the range of moose density estimates from dung counts overlapped both with the REM estimate and the current official estimate. Unfortunately independent density estimates are not available for roe deer, which is also where we observe the largest discrepancies between dung count and REM based estimates. The REM-based density estimate of roe deer was consistently more than double that of dung counts even when considering variation in defecation rates. The density estimate based on dung counts may be influenced by not only the detectability of pellets, but also by the correct identification of pellet groups, given the diverse ungulate community in our study area and overlap in dung morphology.

The encounter rate of pellets of differently sized ungulates, and correct species classification, are important considerations when designing dung count surveys. The larger and more distinct moose pellets are easier to detect than the pellets of roe deer, especially in areas with dense ground vegetation (Lioy et al. 2015). This might explain why the density estimates for moose were fairly similar among methods, especially after accounting for possible variation in defecation rates. However, failing to detect pellets and misclassifying species would bias population densities for smaller species. This may explain why roe deer estimates from dung counts were consistently lower than the REM-based estimates, even after accounting for variation in daily defecation rates. Furthermore, a high level of empirical knowledge and experience is required to assign pellet groups to a species in the field (Smith 2012). The classification threshold of 45 pellets suggested by Edenius (2012) needs further testing and may have resulted in a proportion of pellet groups being assigned to the wrong species. Dung morphology may not only overlap for roe deer and fallow deer, but also for red deer (Kohn and Wayne 1997), given the low number of encountered pellet groups, but relatively high number of camera images. Further studies are needed to validate field identification methods for ungulate dung, especially for similar species with overlapping ranges. One possibility would be to validate morphometric differences as done by Bowkett et al. (2013). Alternatively, molecular methods like DNA barcoding are rapidly becoming more affordable and could offer an alternative for morphometric identification of species (Waits and Paetkau 2005). It is in these instances that the ability to identify species from camera trap images may provide an important tool for estimating densities in multi-species ungulates communities.

Recent technical and methodological advances have made camera trapping an attractive alternative for estimating ungulate densities, particularly since the REM removed the need for individual recognition. The method produced density estimates with similar percentage relative precision (see Table 1) when using raw estimates for ADD and ADA from photos as when accounting for detection probability, that is, incorporating EDD and EDA (Rowcliffe et al. 2011). Variation between species-specific density estimates averaged around 0.05/km^2. One could argue that EDD and EDA might vary due to differences in the field of view of the two camera models used. However, models including camera type as covariate did not generally perform better than models without.

Since ADD and ADA are simple means, their calculation is arguably more straightforward than modelling EDD and EDA. This may make the former more convenient to use for citizen scientists, for example, local hunting or conservation groups interested in adopting camera traps for monitoring ungulate populations. Our results suggest that in this instance the simpler approach would not compromise the quality of the estimate. In order to improve the precision and accuracy of variables extracted directly from the camera trap footage, a detailed grid of distance markers as suggested by Caravaggi et al. (2016) could be adopted. Additionally, distances and angles could be estimated in classes rather than exact numbers (Hofmeester et al. 2017). However, in our study the much simpler application of markers at only three distance classes away from the camera resulted in realistic density estimates. Again, this simpler alternative to the labour intensive detailed grid may be preferable when involving volunteers in monitoring.

The method estimating daily distance travelled had a large impact on density estimates from the REM. Even after accounting for GPS positioning intervals, daily distance travelled for moose based on telemetry data was 2.08 km/day and resulted in much higher density estimates than those resulting from the camera trapping with 8.59 km/day. A similar trend is visible for roe deer where daily distances travelled based on telemetry data were 4.22 km/day and 11.90 km/day from the camera trapping. These observations correspond well with Rowcliffe et al. (2016) findings that camera-based estimates of day range were between 1.9 and 7.3 times higher than those indicated by telemetry data. As an explanation, they suggested that distance travelled can be prone to underestimation when extracted from tracking data in which spatial locations are not fixed frequently enough to capture fine-scale movements. In fact, Rowcliffe et al. (2012) showed that one would need several fixes per minute to include detailed micro-movements to arrive at accurate estimates of day range. These micro-movements were visible on pictures of the camera trapping which would explain the higher estimates of daily distance travelled for both species. Thus, our 30-min and 1-h recording intervals from GPS data might still have been too long, which is also suggested by the shape of the regression line (Fig. 3). One would expect the slope to level off at very high fix frequencies, but for our data the slope remained steep close to the intercept. Therefore, telemetry data may have underestimated the true day range of moose and roe deer in our study, although considerable individual variation exists. This may be inconsequential in migration studies focusing on large-scale movement patterns, but can severely bias the REM density results. Given the potential importance of this bias, future methodological studies need to focus on disentangling sources of error in daily movement when comparing cameras and telemetry.

Our sampling strategy was largely random although some cameras were slightly biased in the direction they were pointing. Since ungulate densities are rather low in our study system, we wanted to ensure that cameras pointed towards locations where capture of ungulates was possible. Thus, our first criterion was to ensure visibility for *c.* 10 m in front of the cameras lens as close as possible to the predefined locations. We did not have enough capture events of red deer and especially not of fallow deer, while dung counts suggested that they do occur at reasonable numbers. Moreover, we regularly observed fallow deer in the southern part of the study area while conducting fieldwork. Our pellet counts as well as previous studies suggest that fallow deer frequently leave forests to feed in open habitats (Putman 1996). Only 2 of the 132 camera locations were in fields or meadows. Since fields and open areas were mostly located close to public roads or houses, we were not able to mount cameras close to our coordinate location since the camera permit required a minimum distance of 100 m to human activity centres. This could explain why our camera trapping was unsuccessful for fallow deer. A more stratified approach to camera placement that incorporates all available habitats would improve future studies.

In conclusion, our results suggest that using camera traps may be a viable alternative compared to classical monitoring methods, and may be especially advantageous to monitor multi-species guilds. We show how a straightforward method of parameter estimation (ADD & ADA) for the REM leads to reliable density estimates exemplified by our deer species data. Our field setup can be used for developing citizen science-based programmes, where non-governmental organizations and interest groups collect the data and public agencies verify the analysis via web-based applications. Similar citizen science-based programmes are already part of today's management (Singh et al. 2014) to keep track of the rapidly changing

European wildlife landscape. We suggest the next logical step is to include camera trapping into those successful programmes.

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Conflict of Interest

The authors declare no conflict of interest.

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Supporting Information

Additional supporting information may be found online in the supporting information tab for this article.

Table S1. Differences between the two camera types.

Table S2. Estimated percentage of time spent active (daily activity level) for moose and roe deer in Northern Sweden. Estimates are based on the distribution of camera trap footage over the daily cycle.

Figure S1. Activity patterns as captured by distributions of camera trap records of (A) moose ($n = 54$) and (B) roe deer ($n = 69$) in Northern Sweden. Grey bars represent detection frequencies, black curves the fitted kernel distributions and black dashed curves the confidence limits.

